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Nycteris thebaica.

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Nycteris Geoffroy and Cuvier, 1795

Nycteris Geoffroy and Cuvier, 1795:186. Type species *Vespertilio hispidus* Schreber.
Nicteris Desmarest, 1803:501.
Petalia Gray, 1838:494. Type species *Nycteris javanicus* Geoffroy.
Nycterops Gray, 1866:83. Type species *Nycterops pilosa* Gray = *Vespertilio hispidus* Schreber.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Nycteridae, Genus *Nycteris* Geoffroy and Cuvier, 1795 (Simpson, 1945). This family contains one genus with 14 species. A key to species of *Nycteris* follows Van Cakenberghe and De Vree (1985, 1993*a*, 1993*b*, 1998) and uses discriminant functions when geographic distribution or diagnostic characteristics do not uniquely identify species:

1 Posterior lower premolar small, its tip reaching about to cingulum of anterior premolar; no marked concavity at center of posterior margin of tragus 2
Posterior lower premolar large, its height about equal to that of anterior cusp of first molar; marked concavity at center of posterior margin of tragus 11
2 Upper incisors trifid; tragus small (*hispida* group) 3
Upper incisors bifid; tragus large 6
3 Size very large; forearm 51.6–64.5 mm; greatest length of skull 23.3–27.5 mm; only occurring in central and western African rainforests and in eastern African coastal forests .... *N. grandis*
Size moderate; forearm 32.8–44.5 mm; greatest length of skull 15.3–18.4 mm; occurring in central and western African rainforests, eastern African coastal forests, and savanna areas 4
4 Occurring in northeastern and eastern African savannas and coastal forests of eastern Africa 5
Occurring in the central and western African rainforests and savanna areas .... *N. hispida*
5 Size slightly larger; forearm 37.3–44.5 mm; condylobasal length 14.6–15.9 mm; maxillary toothrow 5.7–6.2 mm; mandibular toothrow 6.4–7.5 mm .... *N. aurita*
Size slightly smaller; forearm 34.8–43.4 mm; condylobasal length 13.2–15.0 mm; maxillary toothrow 4.8–5.8 mm; mandibular toothrow 5.4–6.6 mm .... *N. hispida*
6 Tragus with squared or flattened top (*macrotis* group) 7
Tragus inverted pear shaped or pyriform (*thebaica* group) 8
7 Forearm 36.1–41.9 mm; condylobasal length 14.0–16.1 mm; very rare species, scarce records from Cameroon, Ethiopia, Zambia, and Zimbabwe .... *N. woodi*
Forearm 39.9–54.8 mm; condylobasal length 16.4–19.6 mm; common species in rain forest and savanna areas of western, eastern, and northeastern Africa .... *N. macrotis*
8 Occurring in west African savanna areas 9
Occurring over the remaining part of Africa, south of the Sahara, along the Nile River, on the Arabian Peninsula, and Morocco 10
9 Size slightly larger; forearm 39.2–47.4 mm; condylobasal length 15.8–17.5 mm; mandibular length 11.8–13.2 mm; mandibular toothrow 6.2–7.4 mm; length of metacarpus of third finger 28.9–36.1 mm; length of tibia 20.3–24.9 mm; the following combination of measurements >21.7: (1.153 × length of maxillary toothrow + 0.187 × width across the upper canines + 0.557 × width across posterior upper molars + 0.657 × mandibular length + 0.395 × length of mandibular toothrow) .... *N. thebaica*
Size slightly smaller; forearm 35.1–44.0 mm; condylobasal length 14.2–16.5 mm; mandibular length 10.4–12.2 mm; mandibular toothrow 4.6–6.9 mm; length of metacarpus of third finger 26.4–32.1 mm; length of tibia 17.0–22.3 mm; the following combination of measurements <21.7: (1.153 × length of maxillary toothrow + 0.187 × width across upper canines + 0.557 × width across posterior upper molars + 0.657 × mandibular

FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of male *Nycteris thebaica* (Royal Ontario Museum collection number 38410). Greatest length of cranium is 10.8 mm.

length + 0.395 × length of mandibular toothrow) .... *N. gambiensis*

10 Forearm 32.3–50.0 mm; condylobasal length 15.1–18.7 mm; common species with wide distribution .. *N. thebaica*

Forearm >50.0 mm; condylobasal length >19.5 mm; very rare species, only known from the type and paratype from Zinave, Mozambique .... *N. vinsoni*

11 Upper incisors bi- or tricuspid; occurs in the southeastern Asian forest areas (*javanica* group) 12

Upper incisors bicuspid, occurs in the Africa forest areas (*arge* group) 13

12 Forearm 41.5–50.4 mm; greatest length of skull 19.1–20.6 mm; length of mandibula 13.0–14.6 mm; upper incisors dominantly tricuspid; limited to Java and Sumatra .... *N. javanica*

Forearm 46.7–52.8 mm; greatest length of skull 21.0–22.9 mm; length of mandibula 14.8–16.4 mm; upper incisors dominantly bicuspid; occurring on Borneo and Malaysian Peninsula .... *N. tragata*

13 Size smallest; forearm 31.7–37.0 mm; condylobasal length 12.8–14.0 mm; zygomatic width 8.4–9.4 mm; width of braincase 6.5–7.4 mm; length of mandibula 9.2–10.7 mm .... *N. nana*

Size larger; forearm 33.7–48.5 mm; condylobasal length 14.6–18.8 mm; zygomatic width 10.0–12.6 mm; width of braincase 7.3–9.0 mm; length of mandibula 10.1–15.9 m 14

14 Size largest; forearm 44.0–48.5 mm; greatest length of skull 20.2–21.7 mm; length of mandibula 13.8–15.9 mm; length of metacarpus of third finger 33.3–35.8 mm; length of metacarpus of fourth finger 36.2–37.7 mm; very rare species, with some scattered records from the western and central African rainforest .... *N. major*

Size intermediate; forearm 33.7–46.8 mm; greatest length of skull 15.4–20.3 mm; length of mandibula 10.1–14.2 mm; length of metacarpus of third finger 24.5–34.8 mm; length of metacarpus of fourth finger 28.0–37.0 mm; fairly common in the western and central African rainforest 15

15 Slightly smaller; forearm length 33.7–38.0 mm; greatest length of skull 15.4–18.3 mm; condylobasal length 14.6–15.7 mm; length of mandibula 10.1–12.6 mm; occurring in the coastal areas of western Africa, Cameroon, Gabon, northeastern Democratic Republic of Congo (formerly Zaire), and northeastern Angola .... *N. intermedia*

Slightly larger; forearm length 35.4–46.8 mm; greatest length of skull 18.0–20.3 mm; condylobasal length 15.4–18.0 mm; length of mandibula 12.1–14.2 mm; commonest species of the group, occurring over the entire western and central African rainforest area ..... *N. arge*

Nycteris thebaica (Geoffroy, 1813)

Egyptian Slit-Faced Bat

Nycteris thebaicus Geoffroy, 1813:20. Type locality "Thebes near Luxor, Egypt."

Nycteris geoffroyi Desmarest, 1820:127. Type locality "Podor, Senegal."

Nycteris capensis Smith, 1829:434. Type locality "Swellidam, southwest Cape Province, South Africa," as restricted by Roberts, 1951.

Nycteris affinis Smith, 1829:434. Type locality "Grahamstown, eastern Cape Province, South Africa," as restricted by Roberts, 1951.

Nycteris albiventer Wagner (in Schreber), 1840:439. Type locality "Nubia." Restricted to Dongola, Northern Province, Sudan by Koopman, 1975.

Nycteris discolor Wagner (in Schreber), 1840:440. Type locality "Ecklon, South Africa."

Nycteris fuliginosa Peters, 1852:46. Type locality "Boror, 19 km northwest of Quelimane, Mozambique."

Nycteris labiata Heuglin, 1861:5. Type locality "Keren, Bogosland, Eritrea."

Nycteris angolensis Peters, 1871:903. Type locality "Caconda, east of Benguela, Angola," as restricted by Hill and Carter, 1941.

Nycteris damarensis Peters, 1871:905. Type localities "Otjimbingue, Damaraland, Namibia."

Nycteris revoilii Robin, 1881:90. Type locality "Somalia." Restricted to Somalia, north of 10°N, by Moreau, Hopkins, and Hayman, 1946:399.

CONTEXT AND CONTENT. Context same as for genus. Subspecies classification is uncertain. The treatment of subspecies follows Kock (1969), Koopman (1975), and Nader and Kock (1982):

N. t. angolensis Peters, 1871:903, see above.

N. t. brockmani Andersen, 1912:548. Type locality "Upper Sheikh, northern Somalia" (*media* Andersen, 1912 is a synonym).

N. t. capensis Smith, 1829:434, see above (*affinis* Smith 1829, *discolor* Wagner 1840, *fuliginosa* Peters 1852 are synonyms).

N. t. damarensis Peters, 1871:905, see above.

N. t. labiata Heuglin, 1861:4, see above (*revoilii* Robin 1881, *adana* Andersen 1912, *aurantiaca* de Beaux 1923 are synonyms).

N. t. najdiya Nader and Kock, 1982:9–15. Type locality "Diriyah, Saudi Arabia."

N. t. thebaica Geoffroy, 1813:20, see above (*albiventer* Wagner 1840, *geoffroyi* Desmarest 1820, *senegalensis* Hartmann 1868 are synonyms).

DIAGNOSIS. *Nycteris thebaica* is recognized by its large, oval ears (Dobson, 1878; Yom-Tov, 1993) and the deep groove between the nose-leaves, which extends from the nostril to a line between the base of the ears (Herselman and Norton, 1985; Madkour, 1988). Generally, fur of the Egyptian slit-faced bat is lighter in tone than in other nycterids (Rosevear, 1965) and pelage hairs lack medullae (Quay, 1970). The tragus assumes an inverted pear shape (Van Cakenberghe and De Vree, 1998).

GENERAL CHARACTERS. Fur is silky in texture and varies in color from dusky brown or pale reddish brown to uniform gray on the dorsal surface, with a white to whitish-grey belly (Al-Safadi, 1991; Dobson, 1878; Rosevear, 1965). An orange phase has been described (Kingdon, 1974; Rosevear, 1965). Color does not follow a geographic pattern, although animals inhabiting drier areas are lighter (Van Cakenberghe and DeVree, 1998).

Tail is long, contained within an interfemoral membrane (Miller, 1907; Walker, 1968) and, like other nycterids, terminates in a T-shaped cartilage that supports the free edge of the tail membrane (Fenton, 1975; Heist and Schaldach, 1965; Koopman, 1984; Miller, 1907; Walker, 1968). Second manal digit is well-developed and third finger has two phalanges (Miller, 1907; Wassif and Madkour, 1974). Tragus is pyriform (Adam and Hubert, 1976; Fenton, 1975), expanded above, and reaches its greatest width about the middle of the inner margin (Dobson, 1878).

Sagittal crest of the skull is low but clearly developed (Rosevear, 1965—Fig. 1). Mandible is straight. The angular process is rounded and does not project behind the condyle (Madkour, 1987). The coronoid process is distinctly pointed (Madkour, 1987).

Considerable morphological overlap exists between specimens examined throughout this species range. Mean (in mm) and ranges of morphological characteristics for male and female specimens of *N. thebaica* are as follows: greatest length of skull, 19.1, 17.0–21.2; condylobasal length, 16.9, 15.1–18.7; width of shield, 7.5, 6.1–9.0; zygomatic width, 11.1, 9.8–12.9; mastoid width, 8.9, 6.1–10.1; width of brain case, 8.6, 7.5–9.6; length of upper tooth row (C–M3), 6.3, 5.0–7.5; width across upper canines (C–C), 4.7, 3.7–6.0; width across upper third molars (M3–M3), 7.0, 4.7–8.5; mandibular length, 12.5, 10.6–14.4; length of lower tooth row (c–m3), 6.9, 6.0–8.4; length of forearm, 44.5, 34.2–50.7; length of metacarpus of the third finger, 33.0, 28.0–39.7; length of first phalange of the third finger, 23.7, 19.4–27.6; length of second phalange of the third finger, 23.3, 17.0–27.8; length of metacarpus of the fourth finger, 35.1, 26.4–40.7; length of metacarpus of the fifth finger, 35.5, 28.2–42.1; length of first phalange of the fifth finger, 12.7, 9.4–15.4; length of second phalange of the fifth finger, 11.30, 8.4–14.4; length of tibia, 22.0, 16.8–26.5 (Van Cakenberghe and De Vree, 1998).

Ranges of external and cranial measurements (in mm) for *N. t. thebaica* and *N. t. labiata* adults, respectively, from Sudan are the following: length of forearm, 43.0–46.0 (n = 4 females); 39–44 (n = 29 males), 41–45 (n = 26 females); condylocanine length, 17.6 (n = 1 female); 15.7–16.3 (n = 7 males), 16.4–16.7 (n = 5

females—Koopman, 1975). An adult male *N. thebaica* from Bahr-el Ghazal (White Nile) Province, Sudan had the following measurements (in mm): length of body, 51; length of tail, 52; length of ear, 30; length of forearm, 45; body mass, 7.5 g (McLellan, 1986). Females are statistically larger than males (Adam and Hubert, 1976). Means and ranges (in mm) for males and females respectively from Senegal are as follows: length of tail, 53.9, 48.0–61.0; 54.0, 48.0–58.0; length of tibia, 24.4, 22.8–26.0; 25.3, 23.2–27.2; length of forearm, 45.3, 43.8–46.8; 46.8, 44.7–48.1; length of hindfoot, 11.9, 11.0–12.5; 12.2, 11.0–13.0; length of ear, 33.3, 31.0–36.0; 33.6, 30.0–35.5; zygomatic breadth, 10.8, 10.2–11.2; 10.9, 10.5–11.4; condylocanine length, 19.4, 18.7–19.9; 19.5, 18.8–20.1; C–M3, 6.8, 6.4–7.0; 6.8, 6.4–7.0; M3–M3, 7.2, 6.9–7.6; 7.2, 6.9–7.4; and C–C, 4.8, 4.5–5.2; 4.7, 4.5–5.0; body mass (g), 8.7, 6.5–9.7; 9.8, 7.0–11.5 (Adam and Hubert, 1976).

Ranges of external and cranial measurements (in mm) for a small collection (n = 2–6) of specimens of *N. t. capensis* adult males and females, respectively, from Zambia, Tanzania, and Malawi are as follows: total length, 104–107, 103–111; length of forearm, 44.4–46.0, 45–46.5; wingspan, 294–298, 292–307; length of hindfoot, 10–11, 10.5–12; zygomatic breadth, 10.9–11.5, 11.0–11.4; condylocanine length, 17.5–17.9, 17.2–18.1; C–M3, 6.4–7.1, 6.4–6.8; M3–M3, 6.9–7.8, 7.3–7.5; body mass (g), 10.3–12.0, 10.3–12.0 (Ansell, 1986*a*). Mean and range of external and cranial measurements (in mm) for *N. thebaica* adults and subadults old enough to fly in Malawi are the following: total length, 100.4, 87.0–114.0; length of tail, 51.9, 48.0–58.0; length of tibia, 24.0, 21.0–25.5; length of hindfoot, 10.9, 10.0–12.0; length of forearm, 45.0, 40.5–47.0; wingspan, 283.0, 270.0–294.0; length of ear, 32.3, 30.0–34.0; maximum length of head, 20.5, 19.0–22.0; length of tragus, 9.2, 8.0–10.0; body mass (g), 9.1, 7.0–12.0 (Happold et al., 1987). Mean and range of weights (g) of adult *N. thebaica* in Zambia are 11.9 and 9.4–16.8 (Whitaker and Black, 1976). Mean weights (g) of specimens from Atlantica, Zimbabwe are as follows: 10.9 (n = 9 adult males), 11.2 (n = 4 post-lactating females), 10.2 (n = 6 juvenile males), and 10.5 (n = 2 juvenile females—Fenton, 1975). In the Transvaal, South Africa, means and ranges of external and cranial measurements (in mm) of adult *N. thebaica* males and females, respectively, are as follows: total length, 113.3, 90–125; 110.6, 98–117; length of tail, 54.9, 48–63; 52.8, 44–57; length of forearm, 47.9, 42–51; 46.7, 44–49; length of hindfoot, 10.8, 9–12; 10.7, 9–12; length of ear, 33.3, 28–38; 33.1, 28–39; body mass (g), 11.6, 7–16; 10.3, 9–14 (Rautenbach, 1982).

DISTRIBUTION. *Nycteris thebaica* occurs throughout Africa, Israel, and the Arabian peninsula (Bodenheimer, 1958; Ellerman et al., 1953; Findley and Black, 1983; Kingdon, 1974; Meester et al., 1986; Nader and Kock, 1982; Qumsiyeh, 1985; Rosevear, 1965; Vielliard, 1974—Fig. 2). This species ranges as far north as Egypt (Makin, 1976; Nader, 1975; Toschi, 1954) and Morocco (Brosset, 1963; Hayman and Hill, 1971; Koopman, 1970; Toschi and Lanza, 1959), and to the southern edge of the African continent (Grobler and Braack, 1985; Stuart et al., 1987). No fossils of *N. thebaica* are known.

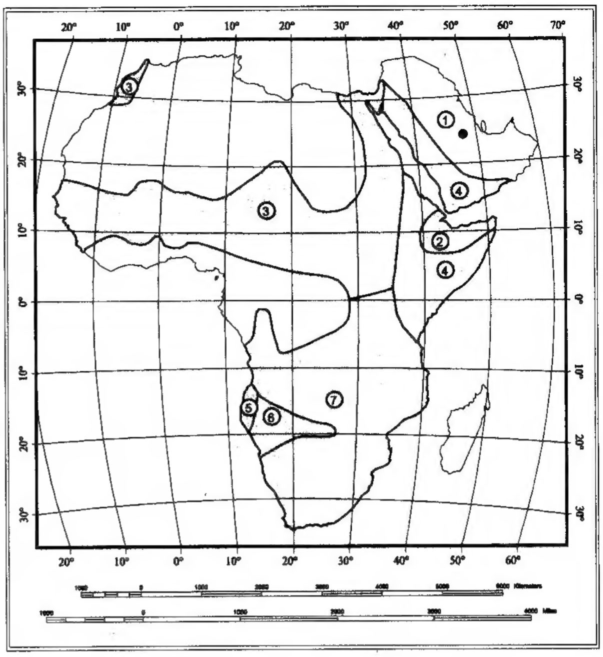

FIG. 2. Distribution of *Nycteris thebaica*: 1, *N. t. najdiya*; 2, *N. t. brockmani*; 3, *N. t. thebaica*; 4, *N. t. labiata*; 5, *N. t. angolensis*; 6, *N. t. damarensis*; 7, *N. t. capensis*.

FORM AND FUNCTION. The Egyptian slit-faced bat has a large wingspan, tail membrane, and ears, and a low aspect ratio (5.5) and wing loading (6.3—Aldridge and Rautenbach, 1987; Norberg and Rayner, 1987). Thus, the bat can maneuver well at low flight speeds in cluttered habitats (Norberg and Rayner, 1987).

Neural arches on cervical vertebrae are thin and provide little skeletal protection for the back of the neck (Fenton and Crerar, 1984). Neural spines are present only on the axis. Posteriorly directed projections from the ventral surface fit into corresponding hollows in the anterior edge of the next vertebra. Projections on vertebrae 1–6 form a morphological gradient, with the largest on the anterior vertebrae (Fenton and Crerar, 1984). The seventh cervical vertebra has no projections and resembles the first thoracic vertebra; these two vertebrae are not fused. Wide lateral processes occur on cervical vertebrae 3–6 but are absent on the seventh. The maximum dorsal and ventral lengths (in mm), respectively, of cervical vertebrae 3–7 for one specimen are, 0.8, 1.9; 0.6, 1.7; 0.5, 1.4; 0.4, 1.3; 0.5, 1.1 (Fenton and Crerar, 1984). The sacral-pseudosacral region forms a cylindrical structure in which the posterior edge is level with the lower border of the acetabulum. Transverse processes of the sacral vertebrae are fused and attach the ilia to the pelvic girdle. Sacral vertebrae are followed by two pseudosacrals (Wassif and Madkour, 1973). The epipubic process is hook-like and the triangular-shaped obturator foramen is relatively large (Wassif and Madkour, 1973). A symphysis pubis occurs in males but not females. The ratchet-shaped os penis is long, slightly curved, and possesses a dorsally excavated oval basal plate (Wassif and Madkour, 1972). The terminal part of the style is thimble-shaped.

The radius is the longest forelimb bone and is slightly curved in its proximal part. The ulna is slender and relatively short. Shafts of the metacarpals are almost cylindrical. The fifth metacarpal is the longest and the third is the shortest (Wassif and Madkour, 1974). The distal extremity of the humerus has a large entocondyloid tuberosity, is extremely wide transversely, but is flattened anterioposteriorly (Madkour, 1978); it forms about one quarter of the humerus (Wassif and Madkour, 1974). The medial epicondyle projects laterally to form a large protuberance (Madkour, 1978).

Dental formula for *N. thebaica* is i 2/3, c 1/1, p1/2, m 3/3, total 32 (Madkour, 1987; Miller, 1907). Upper incisors are bifid (Fenton, 1975; Koopman, 1984; Madkour, 1987; McLellan, 1986; Rosevear, 1965) and closely resemble lower incisors in size and form (Madkour, 1987). This species has chisel-shaped incisors, pointed canines, and broad, acutely-tubercled molars with w-shaped cusps (Madkour, 1987). The outer lower pair of incisors have a crown; however, they are not as large and distinctly trifid as the other two pairs of incisors (Madkour, 1987; Miller, 1907). Upper incisors are equal in vertical extent and are close together in the center of the space between the canines. The pm4 is very small and almost concealed by pm2 and m1. The third upper molar has a metacone, mesostyle, and three commissures (Madkour, 1987; Miller, 1907). Posterior molars are greatly reduced in size (Madkour, 1987; McLellan, 1986). The crown of the posterior molars on the lower jaw is entirely below the cingula of adjacent teeth (McLellan, 1986). First and second upper molars resemble each other. The crown of each molar is wider than long or high and all have one internal and two external roots (Madkour, 1987). Each upper molar is set obliquely with the outer portion higher than the inner portion (Madkour, 1987). Milk teeth are slender with acutely pointed cusps. They often coexist for a short period with the permanent teeth, when the latter are significantly more elevated above the gum (Madkour, 1987).

Lips are hairy (Madkour, 1988). Two circumvallate papillae are located at the posterior end of the tongue (anterior to the glosso-epiglottidean fold), and randomly arranged fungiform papillae are located on the tongue margins (Madkour, 1977). Palatal rugae are

located in the post-canine area but do not extend beyond the anterior third of the second molars (Madkour, 1977).

Kidneys are unilobular, classically kidney shaped, and have broad papillae (Happold and Happold, 1988). The ratio of renal medulla to cortex was 3.03–4.64 in three specimens (Happold and Happold, 1988) and suggests that *N. thebaica* cannot produce concentrated urine.

Ovaries are bilaterally flattened ovoid structures (Bernard, 1980). The right ovary is larger than the left (in mm): right ovary, $1.2 \times 0.8 \times 0.5$, left ovary $0.8 \times 0.6 \times 0.3$ ($n = 6$ parous females). The ovary is enclosed in an incomplete ovarian capsule containing a single lateral slit (Bernard, 1980). The ovary has a broad outer cortex and a thin medulla without medullary cords. Large numbers of primordial and primary follicles, fewer developing secondary follicles, and little interstitial gland tissue occurs in the ovaries (Bernard, 1980).

Oviducts are located in the walls of the ovarian capsules; the right oviduct is more tortuous than the left. Each oviduct has an interstitial region that joins the uterine horn and has a simply folded mucosa with a thick submucosal layer, an isthmus region with a more complexly folded mucosa (with about equal numbers of ciliated and secretory cells lining the lumen) and a thinner submucosal muscular layer, and an ampulla region with a highly irregularly folded mucosa, a very thin submucosal layer, and approximately equal numbers of ciliated and secretory cells lining the lumen. The mean lengths (in $\mu m \pm SD$) of lumenal cilia are, 9.4 ± 3.0 (interstitial region), 6.0 ± 1.5 (isthmus region), and 5.4 ± 1.7 (ampulla region—Bernard, 1980).

Uterus is short and wide with long narrow uterine horns (Bernard, 1980; Madkour, 1989). In parous females, the right uterine horn is approximately 50% longer and wider than the left (in mm): right, 2.32–2.91, 1.09–1.32; left 1.66–2.49, 0.83–1.00 ($n = 6$). In nulliparous females, the right uterine horn is longer and wider as well (in mm): right 2.44–2.54, 0.85–0.87; left 2.28–2.36, 0.80–0.83 ($n = 3$—Bernard, 1980). The uterus lacks a separate body. Although the two uterine horns are joined externally, their lumina are distinct and run parallel to each other. The uterine horns are lined with columnar epithelial cells and, in the anestrous condition, the mucosa contains few uterine glands. Two cervical canals open into the vagina. The anterior part of the vagina is flattened dorsoventrally and the distal part is cylindrical (Madkour, 1989). It is lined with stratified epithelial cells throughout its length (Bernard, 1980).

The esophagus is a long, narrow, dilatable tube of consistent diameter (Madkour, 1977). The stomach is mallet-shaped; the cardiac portion is larger than the pyloric region, and the intestine is loosely and irregularly coiled (Madkour, 1977). Average measurements (in mm) for parts of the digestive tract for specimens from Egypt are: esophagus length, 16.9; average diameter, 0.9; stomach length, 10.5; greatest width, 6.1; small intestine, 89.5; average diameter, 1.2; large intestine, 6.5; average diameter, 1.5 (Madkour, 1977).

ONTOGENY AND REPRODUCTION. *Nycteris thebaica* is monotoccus. Tropical populations are polyestrous with a postpartum estrous between pregnancies (Anciaux de Faveaux, 1978*a*; Bernard, 1980, 1982; Bernard and Cumming, 1997; Harrison, 1958; Koopman et al., 1978; Matthews, 1939, 1941). Populations inhabiting subtropical and temperate climates are monestrous and demonstrate a relict polyestrous breeding cycle with a second period of Graafian follicle development towards the end of the gestation period that does not result in ovulation (Bernard, 1980, 1982; Bernard and Cumming, 1997). In temperate South Africa, proestrous occurs in early April and May, estrous in early June, metestrous in mid to late June, pregnancy from June to November, and anestrous from November to April (Bernard, 1980).

Mean mass at birth is 6.0 g (Bernard, 1980). Gestation of subtropical and temperate forms of *N. thebaica* is ca. 5 months, and in tropical climates ranges from 2.5 to 3 months. The fetal growth rate in temperate forms is low, a function of the long 155-day gestation period, but likely is higher in *N. thebaica* females in tropical habitats. The long gestation period may be related to ambient temperatures and/or food supply (Bernard, 1980). In *N. thebaica* from South Africa, superficial, circumferential implantation in the right uterine horn occurs 16 days (10.3% of pregnancy) after mating. From implantation to appearance of the limb buds takes 47 days (30.3%), and from limb buds to parturition takes 92 days (59.4%—Bernard, 1980). Male and female reproductive cycles are synchronized; spermatogenesis in *N. thebaica* in South Africa begins in March, and spermatozoa are released to the epididymides in late May (Bernard, 1980; Bernard and Cumming, 1997).

Females carry non-volant young in flight and may carry their young on normal feeding flights (Ansell, 1986*b*). Females carried young away from the day roost at dusk, a form of predator avoidance behavior (Aldridge et al., 1990). Young weighed about half the mother's weight. Young cling to a mamma during flight (Ansell, 1967).

ECOLOGY. *Nycteris thebaica* is a savanna-palaearctic species that inhabits temperate, subtropical, and tropical zones (Koopman, 1975; Smithers, 1983). The Egyptian slit-faced bat inhabits a variety of habitats (Smithers and Tello, 1976), but prefers open savanna woodland to rainforest (Aldridge et al., 1990; Happold, 1985; Happold and Happold, 1988; Happold, et al. 1987; Kingdon, 1974; Rautenbach and Fenton, 1992; Roer, 1971; Rosevear, 1965).

Nycteris thebaica is a generalist-opportunist that feeds on arthropods (Fenton, 1972, 1990; Fenton and Thomas, 1980; Happold and Happold, 1988; Herselman and Norton, 1985; Miller, 1907; Whitaker and Black, 1976). Orthopterans, lepidopterans, and coleopterans are primary prey (Chapman, 1958; Fenton, 1975; Fenton et al., 1977; Fenton and Thomas, 1980; LaVal and LaVal, 1980; Whitaker and Black, 1976). Homopterans, araneidans, isopterans, neuropterans, hemipterans, hymenopterans, dipterans, and scorpionidans comprise a minor part of the diet (Felten, 1956; Fenton et al., 1977; LaVal and LaVal, 1980). Lepidopteran larvae are increased in the diet during the dry season (Whitaker and Black, 1976).

Diet is influenced by time of year (e.g., rainfall patterns and plant phenology), geographical area (and therefore distribution and abundance of insects), and the condition of the bat (Fenton, 1975; Fenton et al., 1977; Fenton and Thomas, 1980; LaVal and LaVal, 1980; Whitaker and Black, 1976). *N. thebaica* may select prey according to body size, abundance, and ease of location and capture (LaVal and LaVal, 1980).

Egyptian slit-faced bats roost in a variety of structures, including the following: caves; mine tunnels; man-made structures such as buildings, tombs, ruins, military bunkers, wells, masonry fireplaces, road culverts, and pit latrines; tree cavities (e.g., *Acacia albida* and *Trichelia emetica*); root cavities; rock crevices; and aardvark and anthill holes (Adam and Hubert, 1976; Al-Safadi, 1991; Aldridge et al., 1990; Anciaux de Faveaux, 1978*a*; Ansell, 1960, 1986*a*, 1986*b*; Bernard, 1980, 1982; Fenton, 1975; Happold et al., 1987; Herselman and Norton, 1985; Kingdon, 1974; LaVal and LaVal, 1980; Lindeque, 1987; McLellan, 1986; Peterson and Nagorsen, 1975; Rosevear, 1965; Whitaker and Black, 1976; Wingate, 1978, 1985). *N. thebaica* usually hangs free from the roof of the roost by its hind leg or legs (Herselman and Norton, 1985; Shortridge, 1934), with its head facing dorsad at an angle of 90° from the long axis of the body (Fenton and Crerar, 1984).

Considerable variation in roosting patterns (i.e., roost switching) of Egyptian slit-faced bats occurred in Zimbabwe; some roosts were occupied throughout the study period (examined on days 1, 6, and 8 of an 8-day study) whereas others were used sporadically (Aldridge et al., 1990). *N. thebaica* selects relatively cool roost sites (compared to prevailing ambient temperatures) that are large enough to allow them to maneuver while in flight (Aldridge et al., 1990). However, with their ability to maneuver in cluttered environments (Norberg and Rayner, 1987), they can use concavities and indentations in small roosts that other species find difficult to access (Bernard, 1980). Day roosts are used as night roosts in some areas (LaVal and LaVal, 1980). Roost selection and use depends on the availability of appropriate sites and use by other species. For example, *N. grandis* is sympatric and preys upon *N. thebaica* (Aldridge et al., 1990). The two species alternate their use of specific day roosts.

The Egyptian slit-faced bat is gregarious and will form colonies ranging in size from a few to thousands of individuals (Kingdon, 1974). *N. thebaica* roosts with other species. In South Africa, for example, *N. thebaica* shares roosts in caves and mine tunnels with *Myotis tricolor, Miniopterus schreibersii, M. fraterculus, Hipposideros caffer, Rhinolophus simulator, R. clivosus*, and *R. blasii* (Bernard, 1980; Herselman and Norton, 1985; Wingate, 1978, 1985). In the Democratic Republic of Congo, *N. thebaica* shares caves with *M. schreibersii, R. swinnyi*, and *R. simulator* (Anciaux de Faveaux, 1978*b*). In eastern Africa, it roosts in caves with *Rou-*

settus aegyptiacus and *Taphozous perforatus* (Kingdon, 1974), and in Malawi with *R. simulator* and *R. fumigatus* (Happold et al., 1988). *N. thebaica* roosts with *N. macrotis* in Senegal (Adam and Hubert, 1976). Lactating females and young roosted in Egyptian caves with *Asellia tridens* and *T. perforatus* (Qumsiyeh, 1985).

Although the Egyptian slit-faced bat is widely distributed, little is known about its population dynamics. *N. thebaica* migrates, but the factors contributing to migration are little known (Bernard, 1980; Herselman and Norton, 1985; Rautenbach et al., 1988). Migration may result from fluctuating insect populations and the need to increase food intake during the reproductive period (Bernard, 1980).

Nycteris thebaica hosts a variety of parasites, including the following: helminths (Myers et al., 1962; Saoud and Ramadan, 1976); nematodes (Barus, 1973); trematodes (Saoud and Ramadan, 1977*a*, 1977*b*); ectoparasites (Allen, 1939; Anciaux de Faveaux, 1971, 1976, 1978*a*, 1978*b*; Fain, 1974; Loveridge, 1922). *N. thebaica* can be heavily parasitized by a small red acarine which congregates along the margins of the ears and wings and apparently causes the infected individual to damage its membranes by scratching (Loveridge, 1922). Insectivorous bats like *N. thebaica* are the most frequent reservoir hosts of infective nematode larvae of the suborder Spirurata because the nematodes use insects as intermediate hosts (Barus, 1973).

The Egyptian slit-faced bat is difficult to keep in captivity. It eats well, but refuses water, and dies of dehydration (Happold and Happold, 1988; Kingdon, 1974).

BEHAVIOR. *Nycteris thebaica* produces a weak echolocation call and is referred to as a "whispering" bat (Yom-Tov, 1993). Echolocation calls of *N. thebaica* are typical of gleaning bats (Aldridge and Rautenbach, 1987; Fenton et al., 1983). The calls are short and of low intensity (Aldridge and Rautenbach, 1987; Fenton, 1975). They are multi-harmonic calls, with modulated frequency (FM) and a shallow sweep, normally lasting <2 ms (Fenton and Bell, 1981; Fenton et al., 1983). The calls sweep downward, are in the frequency range 61–97 kHz, and most of the energy is at 94 kHz (Fenton and Bell, 1981). *N. thebaica* increases the rate at which it produces echolocation calls as it approaches a target to gather information about the prey and surrounding environment. Interpulse intervals decrease from 22 to 10 ms during approach to facilitate increased feedback (Fenton et al., 1983).

In addition to echolocating calls, Aldridge et al. (1990) identified two tonal calls lasting >40 ms that were audible to researchers. One is a narrow-band call (mean bandwidth 3.8 kHz; mean minimum and maximum frequencies, 8.8 and 12.6 kHz; $n = 78$) emitted in the roost. Narrow band calls frequently attracted other bats to the source. The second is a broadband call (mean bandwidth 11.9 kHz; mean minimum and maximum frequencies, 10.1 and 22.1 kHz; $n = 18$) consisting of a downward frequency-modulated shift (from ca. 22 to ca. 10 kHz) followed by an upward shift (back up to ca. 22 kHz). The bats emitted the broadband call when leaving the roost. The interval between calls averaged 94 ms; however, some narrow-band calls were occasionally terminated with a slight upward frequency modulation, suggesting that the two vocalizations are used together. Use of broadband echolocation calls enables the Egyptian slit-faced bat to orient in cluttered environments.

Multiple feeding strategies are used, including hunting during continuous flight or from perches, and by taking volant and nonvolant prey (Aldridge et al., 1990; Felten, 1956; Fenton, 1975; Fenton et al., 1983; Kingdon, 1974). While perching, the bat scans for auditory cues generated by prey (e.g., those associated with movement). *N. thebaica* hangs upside down by one foot with its head slightly tilted and scans the surrounding area with a combination of head and ear movements and body rotations of up to 180°. Once the bat detects sound, it directs its head toward the source while rapidly moving its ears backwards and forwards. The bat then attacks the source of the sound (Fenton et al., 1983). Vision may be used in association with echolocating strategies to capture prey (Fenton, 1975).

Nycteris thebaica hunts around buildings, sometimes very close to the ground, and in tree canopies (Aldridge et al., 1990; Fenton, 1975; Fenton and Thomas, 1980). This agile bat hovers (Findley and Black, 1983; LaVal and LaVal, 1980) and can pick stationary insects off a variety of surfaces (Aldridge and Rautenbach, 1987); it gleans prey from vegetation, walls, the ground, rock faces, and around lights (Fenton and Thomas, 1980; Happold and Happold, 1988). The Egyptian slit-faced bat does not restrict its foraging to a specific habitat or situation (Fenton and Thomas, 1980); however, it does modify flight pattern to suit the habitat in which it is searching for prey (Aldridge et al., 1990). In general, *N. thebaica* engages in longer, more continuous flights in open habitat than in closed habitat (Aldridge et al., 1990).

Small insects (<14 mm) are consumed immediately and larger prey while hanging from a perch (Fenton et al., 1983; Herselman and Norton, 1985; Lindeque, 1987). This bat envelops ground prey with its wings and uses the interfemoral membrane to deliver food to the mouth (Fenton et al., 1983). When perching, the bat strips the wings from moths, and the posterior legs and wings from grasshoppers and katydids. *N. thebaica* can handle and consume insects up to 30 mm long in <2 min. (Fenton et al., 1983).

In Namibia, the short courtship is characterized by frenzied flying, in-flight head butting, and neck biting (Lindeque, 1987). Copulation is completed while the bats hover and is repeated a number of times.

GENETICS. The diploid number is 42 and the fundamental number is 78. The karyotype of four females and two males from Zimbabwe includes nine pairs of metacentrics, three pairs of subteleocentrics, and one pair of acrocentrics (Peterson and Nagorsen, 1975). The Y chromosome is submetacentric, and the X chromosome is small and metacentric. A pair of metacentric chromosomes has secondary constrictions in one arm of each homologue. In some metaphase spreads, only one chromosome of the pair appears to contain secondary constrictions.

REMARKS. *Nycteris* Geoffroy and Cuvier, 1795 was a nomen nudum (Meester et al., 1986). According to the Rules of the International Commission on Zoological Nomenclature, the correct name of this genus should have been *Petalia* Gray, 1838 (Simpson, 1945). *Nycteris* would then date from Borkhausen (1797) and would be the same genus as *Lasiurus* Gray, 1831. Miller (subsequent to 1907) and others followed this revised nomenclature, but the Commission eventually suspended the Rules (Opinion 111) and made *Nycteris* and *Lasiurus* valid names as used by Miller in 1907 (Simpson, 1945) and as given here.

Although widely distributed throughout Africa, the bat is commonly referred to as the Egyptian slit-faced bat after the country from which Geoffroy (1813) described the species. The specific name *thebaicus* was assigned by Geoffroy to commemorate the locality where it was first collected, Thebes near Luxor on the Nile River.

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